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TRADITIONAL NEO-DARWINISM IS NOT ENOUGH! A HIERARCHICAL - DEMIC THEORY OF EVOLUTION

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A B S T R A C T

In order to answer some oral criticisms to our "critical overview of the synthetic theory" (Hoenigsberg, 1988), the author attempts to review, as a summary, what the most frequent question demands: "what is left out of the New Synthesis"?

R E S U M E N

Con el propósito de contestar a ciertas críticas orales a nuestro "critical overview of the synthetic theory" (Hoenigsberg, 1988), el autor trata en estos comentarios muy resumidos la más frecuente de las preguntas "¿qué es lo que la Nueva Síntesis dejó por fuera"?

INTRODUCTION

There are certain historical patterns of evolutionary adaptations that become demic properties in the form of genomic nested sets of pleiotropic and epistatic nature that secure the familiar species properties. Thus, the species level becomes a construct of synapomorphic characters. A progressive relationship of a genealogical hierarchy is the final result of the nested sets of the coadapted interactions that originate in the local population (= deme).

If we do not recognize the deme as the first level of a series of nested gene pools within a series of coadapted - genealogies and hierarchically organized that participates and limits the next hierarchy, the species level, then we would have no way to theorize about the ontogenical hierarchical systems that make of development a predictive cohesive entity within each taxonomic category. Moreover, that concept makes possible recognition of ontogenical homologies similarly nested in higher categories.

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I think the modern synthesis does not explain an evolutionary process that take into account molecular, developmental, demic and species levels and of course, leaving out the several ontologically - based hierarchical systems in life processes. We need a hierarchical theory because nature itself appears so arranged. Sewall Wright (1953, 1964), and after him others, constructed a theory with a hierarchical edifice in mind. Many of us have written about the need for a hierarchically structured theory that can glue together molecules, populations and phyla (Salthe, 1975; Eldredge & Salthe, 1985; Hoenigsberg, 1988).

We assume that the hierarchical levels are constructed as coadapted integrated systems in the local gene pool. Thus, it starts out as an integrated reproductive community, that eventually becomes nested physiologically and morphologically into the next level, the species, and so on into higher monophyletic taxa. Although the abiotic world is not irrelevant to the biotic realm we will not refer to it as the lowest stratum on which the hierarchical system sets its foundation.

We are not saying that the species defined as an eventual discrete reproductive community does not exist or that it is of no importance to a modern evolutionary theory. What we do claim is that there are profound catastrophes and novelties at the ith level that need have no effect at upper nested levels and yet can be limiting within that ith level. Dover (1982) has been asserting that there are a large amount of molecular change within the genome with no discernible effects on the phenotypes. Therefore, from observing the phenotype we have no way to say anything of the stability of the genotype. We believe that what happens at the molecular level (ensymes) can be limiting to what may appear at the organismic level in the deme; and if population geneticists have not found evidence of this nested constraint can be attributed to not having dealt with real demes, out in the isolated periphery. Most of the research in population genetics has taken place with biological models that live in the central part of the distribution of any species. Thus, the real demic structure have not emerge from such works.

In our theory each category is an entity at a different level that do not have to directly interact in each dynamic process of the previous level. However each level constrains the previous one nested into it. Thus, their genetic relatedness affects the degree of effectiveness across contiguous levels of each constraint. And finally their importance diminishes as the levels involved are increasingly remote. There are in our view admitedly conceptual analogies with the familiar Linnaean hierarchy of Taxonomy. Ours, however, being systems of nested coadapted integrated entities do not vanish but rather constitute constraints that maintain

their permanence in each category. Each level emanate elements of constraint for the next hierarchy, but of course, been the result of complex interactions that initiate in the local gene pool they cannot result in precise sets of nested characteristics for each subsystem from which they originated.

We are, of course, grateful to our intelectual predecesors (Gerard, 1958; Bertalanffy, 1968; Valentine, 1968; Bonner, 1969; Bunge, 1979; Koesler, 1967, 1978; Dover, 1982; Salthe, 1975). Our situation resembles Simpson's taxa and taxonomic categories (Simpson, 1961). Each level in our view is an independent entity by itself although it is a part of the next category, just as demes are not simply members of species, as the synthetic theory wants them to be, they are demes and the next organizational level, the species, are species, and so on to genera and higher categories.

THE GENEALOGICAL HIERARCHY AND THE DEMIC THEORY

Saying that organisms are related in evolution is like saying that they are firstly genetically and finally genealogically interconnected. It means that each species as a set of nested taxa and synapomorphics being shared by ancestry and descendants are the phenotypic threds that bind together nested monophyletic taxa. In the local gene pool pleiotropic and epistatic interactions are the material genetic tools of genealogical hierarchies. Local environmental insults and the first level of ecological hierarchy interact producing the material basis for the genealogical construct. The local result is the deme with its first genetic coadapted hierarchy that if reproductive isolation does not appear it will be a candidate for a nested set of characteristics within the next category. Usually vagility, colonization, extinction, the degree and rate of migration and mutation determine the emergence of sexual isolation. Sometimes, geographic isolation and marginality will result in sexual isolation.

In *Drosophila pseudoobscura* from the altiplano cundiboyacense such isolation has initiated (Hoenigsberg *et altri*, 1988; Hoenigsberg & Cárdenas, 1989, this Journal) with more or less similar mechanisms throughout the area, but their degree of morphological similarities and symmetrical correlations in sexual combs, vaginal bristles, and wing lenghts have significantly diverged from each other (Alvarez *et altri*, 1989, this Journal). However, they appear, in what is useful for reproduction, still nested within the species *Drosophila pseudoobscura*. Sochagota, Potosí, Recreo and Aguas Calientes as local demes of the altiplano cannot be considered

as having the same set of synapomorphic characters nested within the species or the "cluster".

CREATIVITY AND GENEALOGICAL HIERARCHY

From several recent publications on biological hierarchies (Eldredge, 1982; Gould, 1982) we can see that there is interest in considering the species both as classes and as individuals. As classes, species belong to the Linnaean abstraction, as individuals, and as demes, they are the real natural entity capable of adaptation and of evolutionary change as groups. As such they are spatiotemporal entities with an initiation, a history and an end; but also with properties unique to themselves. Some of their species-specific characteristics may emerge from other nested demes, although not necessarily by simple addition of properties from the previous level; in fact some diagnostic features may be new as the result of creative properties accrued from demes and various populations. What the Neo-darwinian theory does not consider as a contributing element of evolution is the spatiotemporal entity of the demes which, at the same time, are part of the Linnaean biological species. The demes, being a part of a discrete reproductive community but not having as yet, diverged sexually from the rest of the species, partakes in the historial pattern created by the two hierarchically organized processes; the genealogical and the ecological history. These two processes interact in the deme and when they regulate their reciprocal dependence they become the first level of the hierarchy which, with other similar demic structures, constitute the nest for the species organization. The degree of coadaptation constructed in each deme and the proportion of genes that each partial or local coadaptation shares with the rest of the mendelian connubium constitutes the case of the species-specific genealogy. Since it results from genetic-environmental interactions the species-specific share of common genetic interactions constitute the thred that provide cohesion and significance to the whole species. The instrument that makes possible sharing a "genetic milieu" is the reproductive plexus that include, to a greater or lesser degree, various demes. However, the reproductive plexus that embraces the whole species, and here we find ambiguity, does not present itself in reality in peripheral and isolated populations. There we have found that many local populations (genealogically demes) have already sufficient divergence among themselves. This incipient split with little migration but much extinction and recolonization of a few couples (small effective size) (Hoenigsberg & Dobzhansky, 1987) are evidence of limited reproductive connubia.

Taxa of higher rank than species, the monophyletic taxa, continue to propagate the previous nest although as separate species already since they are not part of the same reproductive community. However, they carry with them that part of the genealogical hierarchy as a block of genotypes as long as they are essential to the adaptive purpose of the group. Higher than species taxa cannot be, of course, spatiotemporal entities, as demes and individuals were.

There are levels of organizations below the organismic one. The organismic level include demes, species and monophyletic taxa. Below this organismic level there are other evolutionary entities: the codons and their base-pairs of the DNA crystal. They organize themselves according to biochemical forces implicated in their chemical bounding. However, below this last level we only find chemical entities that are not explicitly and directly implicated in organic evolution.

However, what concerns us now involves codons-chromosomes-individuals-demes-species and monophyletic taxa as far as the proportion of shared genealogy meaningful to the evolutionary process. We, of course, have to insist on that fraction of hierarchical nest that each level shares with the other because they are part of the nest, a "cassette" if you prefer. The deme standing in between the lower molecular level and the higher species and monophyletic taxa levels necessarily become the carrier of the shared patrimony. Whatever increases or decreases demic cohesion by increasing or decreasing its homeostatic processing will infringe on its possibilities to transmit to the next hierarchical level the original genealogical and nested patrimony. If peripheral and isolated demes with conditions, like geographic distance from the main part of the species distribution lacking migrations among the demes with small effective sizes and frequent local extinctions, obligate consanguinity, that as an overall result diminish the number of alleles per locus we have conditions propitious for lowering group homeostasis. Such demes will tend to diverge their "cassette" because it does not fit with the rest of the species. This process does not have to be gradual, even single mutations may bring forth "departures". The local deme pool becomes highly sensitive when it has lost its homeostatic capacity in generalized homozygosis: this is a highly creative moment for the species when new "things" can happen. Some chromosome rearrangements and other departures from homologous compatibilities can also be rather unsettling for the peripheral and isolated deme (see Hoenigsberg, 1989 this Journal).

Drosophila pseudoobscura from the altiplano Cundiboyacense is the only sure example that we know of a peripheral and isolated population. Its depauperated variability and its highly "disturbed" morphologies (com-

pared with Davis populations) showing, for each of the six demes studied throughout, different sexual-combs, numbers and patterns in each deme plus a highly uncorrelated left-right pattern (multiple regression analysis have revealed this unpredictive right and left sides) for wings and for vaginal bristles, give as an overall picture sufficient examples of unsettling new demic structures. We postulate that the original hierarchical nest of the central part of its distribution have lost its homeostatic cohesion! (l.c., Alvarez *et altri*, 1989, this Journal).

The local coadaptation within demes does not oppose homeostatic, although in peripheral isolates the local gene pool having to reorganize itself around new and changeable means, with rather large variances and relatively large coefficients of variants (l.c., Alvarez *et altri*, 1989) are conditions that facilitate either the destruction of previous homeostatic networks or at least the danger of loosing it up specially for characteristics whose differences depend more on epistatic regulatory interacting genotypes than on additive structural ones. In our demic theory, demic genotypes as a network of local coadaptations nested within the species genotypic structure always are within the hierarchical domain that the species structure allows. The allowance of the species will necessarily depends on its genealogical and ecological history every where in its distribution, including in its peripheral incursions. For this reason it will always escape mathematical predictive models because in some historical moments the species structure will be strongly cohesive and well buffered against the peripheral propagules thanks to constant hybridization and its large demographic units, while in other species structures genealogical and ecological history have not as strong cohesive and possibly even poorly buffered networks that will not resist peripheral "shake ups".

POPULATIONAL CONSTRAINTS

In our view each individual of each deme carries within it a representation of its relations to other members of the deme and at the same time to its wider environment and the ecosistem to which it belongs through the general genome of the deme. Therefore, with such a complex blueprint in which both its organismic entity and its populational one fuse into one, the morphological, physiological and behavioral presence become a three dimensional representation of the various levels through which it must accrue interdependence in order to fully belong to the genealogical and to the ecologic hierarchy that correspond to its deme. This structural solidity of the individual within the demes permits, in our demic theory,

Genetics in 1989 our thanks. However, it was Professor Ernst Mayr's written commentaries and suggestions that made this reply necessary.

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